THE CAPILLARY BED OF THE CENTRAL NERVOUS SYSTEM OF CERTAIN INVERTEBRATES

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The vascular pattern of the vertebrate brain may be either one of two types: the one consists of single vessels that anastomose to form a continuous capillary network; the other consists of paired vessels that end in capillary loops. These two types are, as a rule, mutually exclusive, except in the lungfish, Epiceratodus (Craigie, 1943), and in the salamander, Ambystoma (Craigie, 1938a), where both networks and loops occur. The network pattern is the more common type. It is found in monotremes (Sunderland, 1941) and in all placental mammals, in reptiles with the exception of the lizards, in anuran amphibians, and in the fishes including the hagfish, Myxine. The paired vessels ending in capillary loops are characteristic of the marsupials (Wislocki and Campell, 1937; Craigie, 1938b; Sunderland, 1941), the lizards (Schöbl, 1878; Sterzi, 1904) including Sphenodon (Craigie, 1941a), and the tailed amphibians (Schöbl, 1882; Sterzi, 1904; Craigie, 1938a; 1939; 1940a) including the Gymnophiona (Craigie, 1940b; 1941b). The brain of the lamprey, Petromyzon, is also supplied by loops (Craigie, 1938a).

The study of patterns of cerebral vascularization has been extended here to include invertebrates. In most invertebrates blood vessels do not enter the nervous tissue. There are, however, exceptions. Havet (1916), for instance, in his investigation of the glia cells of the invertebrates mentions the existence of blood vessels within the central nervous system of the earthworm. Another reference may be found in Cajal's (1929) paper on the origin of unipolar neurons in invertebrates according to which the cerebral ganglia of the squid are vascularized by intraganglionic blood vessels.[2] Both of these animals, the earthworm and the squid, have been studied, therefore, and the blood vessels supplying their ganglia have been compared with those of vertebrates.

Material and Methods

Large earthworms (*Lumbricus terrestris* [3]) were collected on lawns in the Cleveland area during rainy nights and were fixed with Zenker-formol. The ring consisting of cerebral and subesophageal ganglia and their connectives was embedded in paraffin and cut 7 micra thick. The sections were stained with Masson's

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[2] The papers of Williams (1902) and Grimpe (1913) give excellent accounts of the vascular system of cephalopodes, but do not include descriptions of the vascularization of the cerebral ganglia.

[3] *Lumbricus terrestris* was introduced from Europe and has become widely distributed in Ohio in the past 25 years (Eaton, 1942).

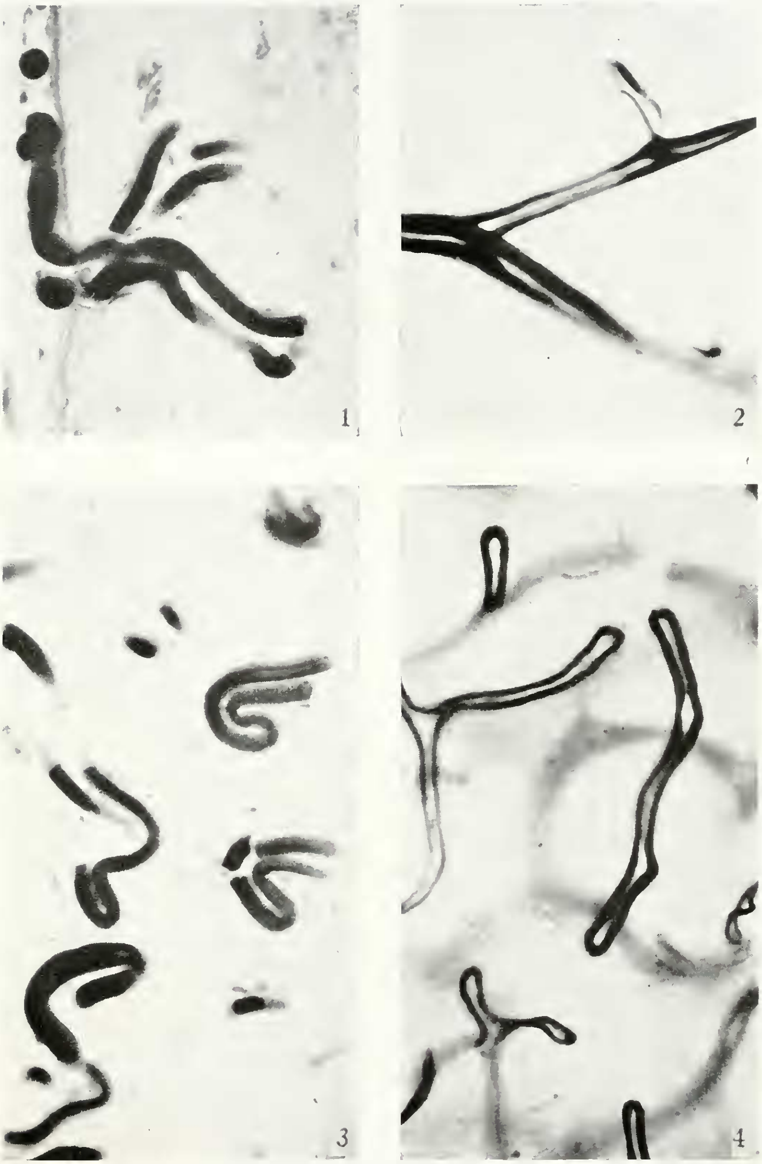

FIGURE 1. A pair of branching blood vessels in the central nervous system of the earthworm. Zenker-formol, paraffin, 7 micra, Masson's trichrome stain. Photomicrograph, × 350.

FIGURE 2. A pair of blood vessels in the brain of the opossum branching in the same manner as those of the earthworm shown in Figure 1. Injection with India ink-gelatin, formalin, nitrocellulose, 100 micra. Photomicrograph, × 350.

FIGURE 3. Terminal loops in the central nervous system of the earthworm. Technique and magnification as in Figure 1.

FIGURE 4. Terminal loops in the brain of the opossum. Technique and magnification as in Figure 2.

trichrome stain. Probably because of the strong contraction of the animals when the fixing fluid is injected into the body cavity, the central ganglia sometimes become very hyperemic. In such animals the blood vessels of the central nervous system are filled with the blood fluid which stains well with the red component of the Masson stain (see Figs. 1 and 3).

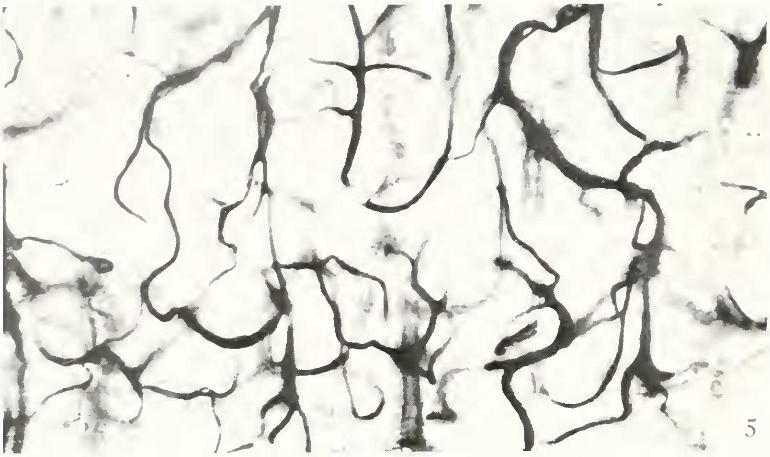

FIGURE 5. Capillary network in the cerebral ganglion of the squid. Injection with India ink-gelatin, formalin, nitrocellulose, 100 micra. Photomicrograph, × 220.

FIGURE 6. Capillary network in the brain of the rat. Technique and magnification as in Figure 5.

Squids (*Logligo pealii*) were obtained at the Marine Biological Laboratory at Woods Hole and were injected with India ink-gelatin through the heart in the same manner as vertebrates. The injected cerebral ganglia were fixed in formalin, embedded in nitrocellulose, and sectioned 100 micra thick. The blood vessels observed in the central nervous system of both the earthworm and the squid were compared with those in various vertebrates, including monkey, cat, guinea pig, rat, opossum, alligator, and several species of teleosts. These were all injected with carmin- or India ink-gelatin, were embedded in nitrocellulose, and were sectioned 100 or 200 micra thick.

Observations

A comparison of the illustrations (Figs. 1 to 4) shows that the blood vessels of the central nervous system of the earthworm are of the same type as those of the opossum brain. In the earthworm blood vessels enter the tissue of the central nervous system in pairs. They divide together and their branches form corresponding pairs (Fig. 1). Finally the two limbs of each pair join and thus end in hairpin-like loops (Fig. 3). This is essentially the same arrangement which Wislocki and Campbell (1937) described in the opossum where arteries and veins stay together in pairs after they have entered the brain tissue. Whenever an artery divides, the accompanying vein divides the same way (Fig. 2), and all blood vessels within the opossum brain end finally in non-anastomosing loops (Fig. 4).

The vascular pattern of the central nervous system of the squid is entirely different from that of the earthworm. In the squid arteries and veins enter the cerebral ganglia singly. Their branches form a network of anastomosing capillaries (Fig. 5), just as in the brain of placental mammals (Fig. 6).

Discussion

"Since the discovery by Schöbl (1878) that there exist in reptiles two radically different types of cerebral vascular bed, one reticular and the other composed of independent, non-anastomosing capillary loops, the relationship between these two types has remained obscure and attempts to reconstruct the phylogenetic history of this mechanism have been complicated rather than simplified by increasing knowledge of the occurrence of the loop arrangement in various vertebrate classes" (Craigie, 1941a, p. 263). The difficulties inherent in the application of the phylogenetic concept to the cerebral vascular patterns are well illustrated by the fact that among the cyclostomes, a group of primitive vertebrates, one (Petromyzon) shows loops, another (Myxine) a network (Craigie, 1938a). The description presented here of loops in the earthworm and of a network in the squid only serves to accentuate these difficulties.

An attempt is made here, therefore, to illustrate a common origin of both systems by dispensing with the phylogenetic aspect altogether. The loop system is not considered as a primitive forerunner of the network pattern, but is presented as the result of a parallel development capable of differentiation and functional efficiency corresponding to that of the reticular type.

The origin of the cerebral vascular system may be compared with that of the endocellular blood vessels in the large extramedullary nerve cells of certain fishes such as the swellfish, *Spheroides maculatus*. In young specimens each one of these cells is surrounded by a network of blood vessels. As the cells become larger in older animals the distance between the center of the cell and the blood vessels apparently becomes too great and the blood vessels enter the cytoplasm. Similarly the whole nervous system while still small could be vascularized by a network of superficial blood vessels (Fig. 7 AB). Such a condition actually obtains in the

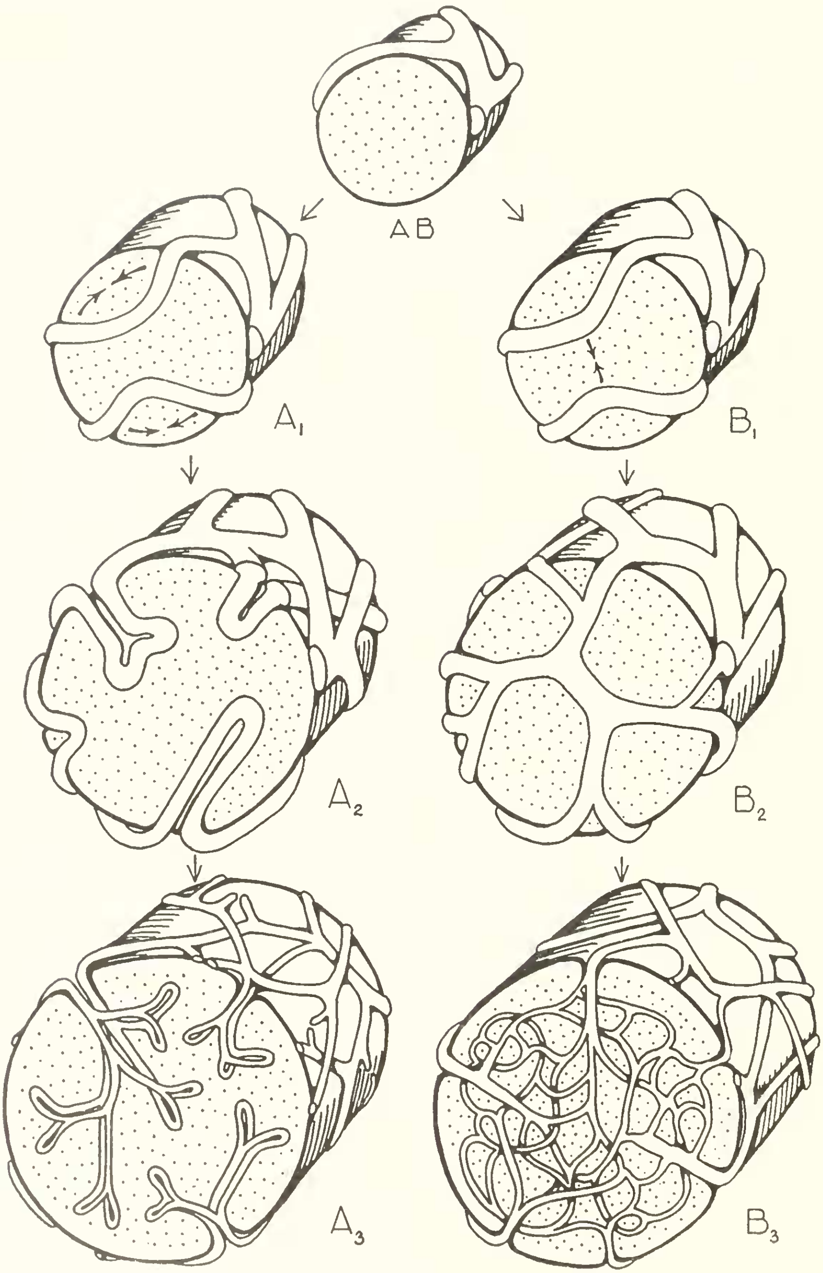

FIGURE 7. Diagram illustrating the derivation of loops and network patterns from a common origin. AB, primitive central nervous system vascularized by superficial network. A_1 and B_1, vessels of the superficial network come to lie within the nervous tissue. There are two possibilities of further development: the blood vessels approach each other in the direction of the arrows (A_1) and thus become paired, or they send out branches which anastomose (B_1). In the one case loops are formed (A_2), in the other a network results (B_2). Both these types are capable of further development to more complex systems (A_3 and B_3).

central nervous system of Amphioxus and in the spinal cord of Petromyzon which are vascularized by networks of superficial blood vessels. With the increase in size of the central nervous system segments of vessels forming part of the surface network come to lie within the nervous tissue (Figs. 7 A_1 and B_1). From this stage both the paired vessels ending in loops (Fig. 7 A_2) and the network (Fig. 7 B_2), may be derived as indicated. Both types occur in invertebrates and vertebrates, and both become eventually highly complex in mammals (Figs. 7 A_3 and B_3).

In this scheme the position of the animal in the phylogenetic order is not considered. This means that the step from A_1 to A_2 or from B_1 to B_2 can be taken anywhere within the vertebrates or the invertebrates. Thus the earthworm follows A_1 to A_2, the squid B_1 to B_2. Among the cyclostomes Petromyzon follows A_1 to A_2, Myxine B_1 to B_2. Epiceratodus and Ambystoma combine the two patterns, a situation which is not illustrated in Figure 7, but which can easily be visualized.

The question still remains: Which factors cause the cerebral blood vessels of the earthworm, of Petromyzon, of the opossum, etc. to differentiate as loops, and those of the squid, of Myxine, and of most vertebrates as a network. An answer to this question is to be expected from the study of the early development of cerebral blood vessels and from the application of the methods of experimental embryology.

Summary

The blood vessels supplying the central nervous system of the earthworm are of the same type as those in the brains of tailed amphibians, lizards, and marsupials, i.e. the blood vessels are paired and end in loops. The blood vessels in the cerebral ganglia of the squid form a network like that which occurs in the brains of fishes, anuran amphibians, reptiles (except lizards), birds, and placental mammals. The origin of both systems is discussed.

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